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Reversed cannibalism, foraging, and surface activities of *Allocosa alticeps* and *Allocosa brasiliensis*: two wolf spiders from coastal sand dunes

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Abstract. Environments where prey availability is scarce or highly variable have been reported as potential settings for the occurrence of paternal investment and sex-role reversal (choosy males and competitive, courting females). *Allocosa brasiliensis* (Petrunkevitch 1910) and *Allocosa alticeps* (Mello-Leitão 1944) are two sand-dwelling wolf spiders that construct burrows along the Uruguayan coastline. Both species present a reversal in typical sex roles and size dimorphism. In the present study, we investigated foraging behavior and population density of both species by performing monthly samplings at the field during one year. Both *Allocosa* are general and highly opportunistic predators, varying their diet according to prey availability. The three most represented common prey belonged to Araneae, Diptera, and Hymenoptera (Formicidae). There were high levels of cannibalism in *A. brasiliensis* and, furthermore, males were observed frequently preying on conspecific adult females. Our discussion of the results based on hypotheses about food limitation and sex-role reversal contributes to our understanding of *Allocosa* species and establishes them as models for future evolutionary, behavioral, and ecological studies.

Keywords: Lycosidae, Uruguay, prey, sex-role reversal, food limitation

Environments with fluctuations in prey abundance and access to refuges or other resources have been reported as potential causes for the evolution of paternal care and sex-role reversed systems (Gwynne 1991; Karlsson et al. 1997; Lorch 2002). *Allocosa brasiliensis* (Petrunkevitch 1910) and *Allocosa alticeps* (Mello-Leitão 1944) are two sympatric and synchronic wolf spider species that live in sandy coasts of Uruguay (Capocasale 1990; Costa 1995; Costa et al. 2006). Individuals reported in studies of Costa (1995), Simó et al. (2005), and Costa et al. (2006) as *Allocosa* sp. belong to *Allocosa alticeps*. The environment these *Allocosa* species inhabit can be eonsidered harsh where prey abundance and weather conditions are highly variable. The changeable environment could be imposing unusual constraints on these species, affecting the sexual behavior of each gender and causing adaptations.

Recent studies (Aisenberg et al. 2007; Aisenberg & Costa 2008) report a reversal in typical sex-roles and size dimorphism for both spider species. Aisenberg & Costa (2008) reported that females are smaller than males, both in *A. brasiliensis* (carapace width, females: 4.63 ± 0.49 mm; males: 5.76 ± 0.59 mm) and *A. alticeps* (carapace width, females: 2.94 ± 0.30 mm; males: 3.28 ± 0.54 mm). The reproductive sexual peak of *A. brasiliensis* and *A. alticeps* takes place in January (Costa 1995; Costa et al. 2006). Females are the roving sexual aggressors that locate and court the males. Copulation takes place inside male burrows and after the final dismount, males abandon their burrows, leaving them to the females (Aisenberg et al. 2007; Aisenberg & Costa 2008).

Allocosa brasiliensis and *A. alticeps* are the sole wolf spiders adapted to living in the Uruguayan coastline (Costa et al. 2006). Food limitation could be an important factor affecting female and male feeding strategies in both lycosid species. Furthermore, occasional field observations suggested the occurrenee of cannibalism of females by males of *A. brasiliensis* during the reproductive period (F.G. Costa and A. Aisenberg, pers. obs.), a phenomenon considered unknown for spiders (Elgar 1992; Wise 2006). Both *Allocosa* species inhabit areas that have been drastically reduced in the last sixty years (Costa et al. 2006), possibly affecting population densities and competition for prey or other resources. In the present work, we studied feeding and surface activities of *A. brasiliensis* and *A. alticeps* with the hypotheses that both species are generalists with high levels of intraguild predation as adaptations for prey unpredictability and intraguild competition in these coastal habitats.

Foraging samplings took place over the course of 11 mo (June 2007–April 2008) in the coastal sand dunes of Marindia (34°46′52.3″S, 55°49′29.6″W), Salinas (34°46′59.8″S, 55°49′51.5″W), Canelones, and Paso del Molino (34°16′ 40.10″S, 55°14′00.80″W), Lavalleja, Uruguay. For 1 h after dark, four to six researchers using headlamps collected *Allocosa* spiders and any prey they had captured. Feeding spiders and prey were captured and taken to the laboratory for identification. Prey were identified to family, and in the case of Araneae and Hymenoptera, to genus. We considered any prey that was primarily consumed so that identification was unfeasible as "unidentified prey."

Surface activity was studied monthly in Salinas from June 2004 to April 2005, for 2 h after dark, using headlamps. We considered the presence of *Allocosa* individuals walking as an event of activity. We labeled as "sea-side" the side of the dune which faced the sea-front; the opposite side was designated as "land-side." Spiders were sampled in four plots of 5 m × 5 m (two plots on the sea-side and two on the land-side) that were drawn parallel to the line of the coast, on the first line of dunes. Additionally, in the period between December 2004 and April 2005, we recorded surface activity as reported previously and related it to the presence/absence of vegetation on the plot. We identified and sexed the individuals in the field. Voucher specimens of both species were deposited in the

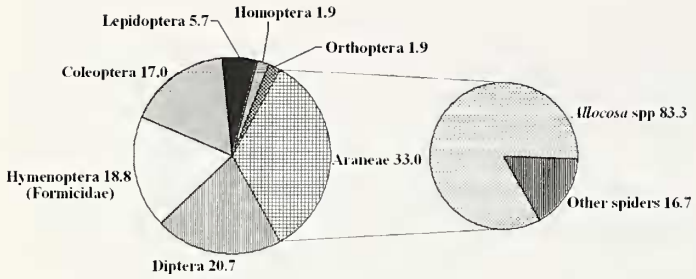

Figure 1.—Prey captured by individuals of both *Allocosa* species, with the corresponding percentages (n = 50).

arachnological collection of Sección Entomología, Facultad de Ciencias, Montevideo, Uruguay.

We recorded 45 individuals of *A. brasiliensis* and 9 individuals of *A. alticeps* feeding during the sampling periods. Most of the diet consisted of spiders, represented mainly by other *Allocosa* individuals. *Allocosa* spiders also preyed on Diptera, Hymenoptera, Coleoptera, Lepidoptera, Homoptera, and Orthoptera individuals but in lower frequencies (Fig. 1). The Hymenoptera captured were worker *Acromyrmex* and *Dorymyrmex* ants, caught on their trails. We found a high rate of intraguild predation in *A. brasiliensis* (Fig. 2). Surprisingly, though females and large juveniles of *A. brasiliensis* preyed on small conspecific juveniles and on adults or juveniles of *A. alticeps*, adult males of *A. brasiliensis* preyed frequently on females of their own species (Fig. 2).

We observed 37 *Allocosa* individuals on the land-side of the dunes and 9 on the sea-side. Surface activity and prey capture showed higher values between December and January, while a lower intensity of feeding was registered in the period between June and November (Fig. 3). We found 13 individuals of *A. brasiliensis* in areas without vegetation and 5 in areas with vegetation. *Allocosa alticeps* did not show preference for areas with (u = 9) or without vegetation (u =6).

The present results indicate that the diets of both *Allocosa* species are non-specific and highly opportunistic, according to prey availability. The occurrence of the three most represented prey (Araneae, Diptera, and Hymenoptera) was highly variable through the year. Both Diptera and Hymenoptera individuals were frequently caught by *Allocosa* spiders during their nuptial swarms or, in the case of ants, while working on

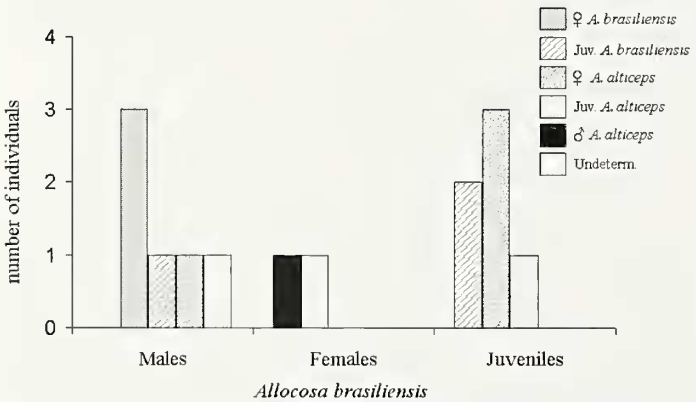

Figure 2.—Number of males, females, and juveniles of *A. brasiliensis* found feeding on individuals of *A. alticeps*, or individuals from their own species.

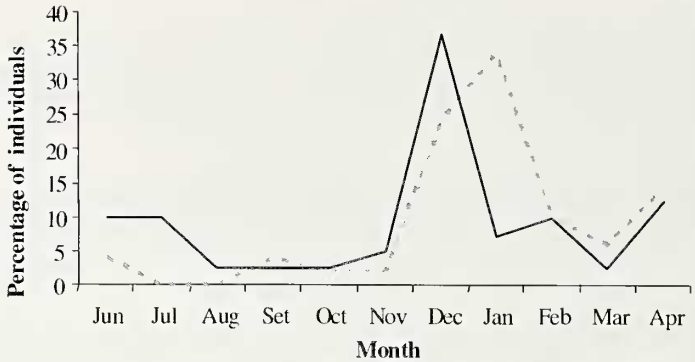

Figure 3.—Phenology of prey capture (dotted line) and surface activity (black line) recorded for both *Allocosa* species (individuals foraging n = 50; individuals walking n = 213).

their characteristic trails. The consumption of ants in natural conditions has been cited for web-building spiders, consisting mainly of winged ants but also walking individuals (Carico 1978; Nentwig 1987). Ground-hunting salticids, thomisids, gnaphosids, and oxyopids often show a high percentage of ants in their diets (Nentwig 1987; Foelix 1996) and members of the Zodariidae family are myrmecophages (Foelix 1996; Pékar 2004; Pékar et al. 2008). Moya-Laraño & Wise (2007) reported *Schizocosa* spiders (Lycosidae) feeding on ants under laboratory conditions. However, studies on lycosid spiders in the field report that Collembola, Diptera, Cicadina, Aphidina, and Araneae would be the main prey groups for this family (Nentwig 1987). Moya-Laraño et al. (2002) provide a different list of prey (absence of ants) for *Lycosa tarentula*, another burrowing wolf spider. Ants are considered very abundant in coastal areas, especially during the summer (Costa et al. 2006) and though they can be considered small prey for a spider the size of an *Allocosa*, they are the most predictable prey. The consumption of ants by *Allocosa* spiders could suggest food limitation and the requirement of special adaptations to manage potentially dangerous prey.

The lack of cannibalism and feeding on small prey in *A. alticeps* could be associated with a smaller size and, consequently, lower energetic requirements (Andersson 1994; Blanckenhorn 2005; Foellmer & Fairbairn 2005). On the other hand, cannibalism rates are high in *A. brasiliensis*. Intraguild predation is considered widespread among wolf spiders (Fernandez-Montraveta & Ortega 1990; Wagner & Wise 1996; Moya-Laraño et al. 2002). In general, studies report juveniles feeding on other juveniles, adults feeding on juveniles, or females feeding on males; overall large individuals feed on small ones (Polis 1981; Polis et al. 1989, 1997; Wise 2006). However, we found males of *A. brasiliensis* cannibalizing females of the same species, a phenomenon unexpected for spiders (Elgar 1998; Elgar & Schneider 2004; Wise 2006). Although we observed males cannibalizing females in just three instances (see Fig. 2), this fact is remarkable because observations of this kind in the field are very scarce even in studies with substantial field effort (Moya-Laraño et al. 2002). The consumption of females by male spiders can be considered non-adaptive, in general, in terms of losing a potential mate. Males of *A. brasiliensis* are sedentary, probably remaining inside their burrows without feeding for long periods (Costa et al. 2006; Aisenberg et al. 2007). So, after copulation and

before constructing a new burrow, they need to forage intensively. Considering the high concentration of *Allocosa* individuals in some areas and the fact that copulations take place exclusively inside male burrows (Aisenberg et al. 2007), females could turn into a good meal for a hungry and large recently-copulated male without a burrow. This would mean no risks to male paternity, as copulated females stay inside the burrows after copulation and until the emergence of spiderlings (Aisenberg et al. 2007). The cannibalism level increases with increasing size-differences (Polis 1981; Polis et al. 1989, 1997; Elgar 1998; Buddle et al. 2003; Wise 2006), so the larger size in *Allocosa* males compared to females could be favoring this atypical male strategy. Furthermore, males of sex-role reversed species are expected to be choosy (Gwynne 1991; Andersson 1994). Male selection with regard to female size has been cited in *Lycosa tarantula* (L. 1758), another role reversed wolf spider species (Moya-Laraño et al. 2003; Huber 2005). Males of *A. brasiliensis* could exhibit extreme mate choice based on female reproductive or nutritional status: copulate with the female or eat her (Elgar 1992). Adaptive foraging (Newman & Elgar 1991), mistaken identity (Gould 1984), and aggressive-spillover (Arnqvist & Henriksson 1997) hypotheses, already tested in other spider species, require further testing in *A. brasiliensis*.

A. brasiliensis was more highly represented in our samplings compared with *A. alticeps*. This could mean that the first species is more abundant, in contrast to the findings of Costa et al. (2006) based on results of pitfall trapping in the same areas, or the fact that it is less sedentary. Furthermore, *A. brasiliensis* individuals could be more easily detected due to their larger size or their greater presence in more open areas compared with *A. alticeps*. However, present surface activity data needs more exhaustive field work, recording not only surface activity but also burrow density, presence of individuals inside open / closed burrows and marking - tracking of individuals.

In the last century, the coastal landscape of the Río de la Plata and Atlantic Ocean in Southern Uruguay has decreased considerably, especially due to urbanization (Costa et al. 2006). Simó et al. (2005) reported the occurrence of *Allocosa* spiders strictly associated with the presence of sand dunes. The current results suggest that the highest surface and foraging activities of both *Allocosa* spiders coincide with the summer of the Southern hemisphere. During this season, coastal areas are most critically affected by tourism, which could also be impacting negatively on critical phases of the spiders' life cycle. This fact may be considered for adequate management plans for these areas. Simó et al. (2005) also postulated *Allocosa* species as potential biological indicators of human effects on coastal ecosystems, as Marshall et al. (2000) did for *Geolycosa*, another burrowing wolf spider species of coastal areas. Both *Allocosa* species seem to be more abundant on the land-side of the dunes, probably because these areas are more protected against the strong winds typical of the Uruguayan coastline. On the other hand, the burrows of the sea-side could be closed off by the spiders due to the strong wind beating on this side of the dune, thus escaping observers' detection. This behavior has been reported for another wolf spider inhabitant of coastal sand dunes (Gwynne & Watkiss 1975). *Allocosa brasiliensis* seems to be more closely associated with areas without vegetation compared to *A. alticeps*, though we need further studies to confirm the trend. Marshall (1997) reported that *Geolycosa xera arboldi* McCrone 1963, another burrowing wolf spider inhabitant from sand dunes, was more directly associated with areas without vegetation. In the first decades of the twentieth century, dunes of the Uruguayan coast were fixed by human plantation of exotic vegetation as *Acacia longifolia*, *Pinus* spp. and *Eucaliptus* spp., especially on the land-side of the dunes (Costa 1995). Areas with exotic vegetation are associated with invader spider species, so the exclusion of *A. brasiliensis* from these areas could be a mechanism to avoid competition for resources, interference competition, and intraguild predation. Their significance as models for testing sex-role constraints in spiders and their potential as biological indicators make *A. brasiliensis* and *A. alticeps* good candidates for further studies that will make clear the effects of environmental factors on the inhabitants of coastal sand dunes and thus contribute to adequate management plans for these areas.

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